Integrative Zoology 2009; 4: 341-356 doi: 10.1111/j.1749-4877.2009.00175.x

REVIEW

Body size structure of Pleistocene mammalian communities: what support is there for the "island rule"?

Maria R. PALOMBO

Department of Earth Sciences, University of Rome "La Sapienza", Rome, Italy

Abstract

Islands are often regarded by scientists as living laboratories of evolution and an optimal context for the study of forces influencing evolution and diversification. Two main issues have been attentively scrutinized and debated: the loss of biodiversity and the peculiar changes undergone by island settlers, primarily changes in size of endemic vertebrates. Over time, several hypotheses have been formulated to explain the causal mechanism of body size modification. Faunas of those islands where mainland taxa migrate more than once provide the most interesting data to answer the question of whether or not trends of insular taxa result from a predictable response to differences in competition and availability of niches between insular and mainland environments. To contribute to the debate, the body size structure of the Pleistocene mammalian faunas from two Mediterranean islands, Sicily and Crete, were analyzed and compared with the structure of coeval mainland faunas.

The results obtained suggest that: (i) size of endemic species does not directly depend on the area of islands; (ii) evolution and size of endemic species seems somewhat affected by the degree of isolation (constraining colonization from mainland) and physiography (sometimes permitting adaptive radiation); (iii) in unbalanced insular communities, the shift in size of non-carnivorous species largely depends on the nature of competing species; and (iv) body size of carnivorous species mainly depends on the size of the most available prey. Consequently, it is rational to suppose that the body size of insular mammals mainly results from the peculiar biological dynamics that characterizes unbalanced insular communities. Ecological interaction, particularly the intraguild competition, is the major driver behind the evolution of insular communities, leading towards an optimization of energy balance through a change in body size of endemic settlers.

Key words: body size, islands, mammals, Mediterranean, Pleistocene.

INTRODUCTION

New as well as recently sterilized islands provide ecologists with natural laboratories in which to study the colonization, development and establishment of new biological communities, but do not allow us to understand the long-term evolutionary processes that lead towards the peculiar insular ecosystems. Studies carried out on past insular faunas might provide answers to fundamental questions such as what general principles are involved in the evolution of island settlers, and what processes underlie and maintain the basic structure of insular ecosystems.

In response to the special characteristics of insular environments, plants and animals often undergo evolu-

Correspondence: Maria Rita Palombo, Dipartimento di Scienze della Terra, Università degli Studi di Roma "La Sapienza" and CNR, Istituto di Geologia Ambientale e Geoingegneria, Piazzale A. Moro 5, 00185 Roma, Italy.
Email: mariarita.palombo@uniroma1.it

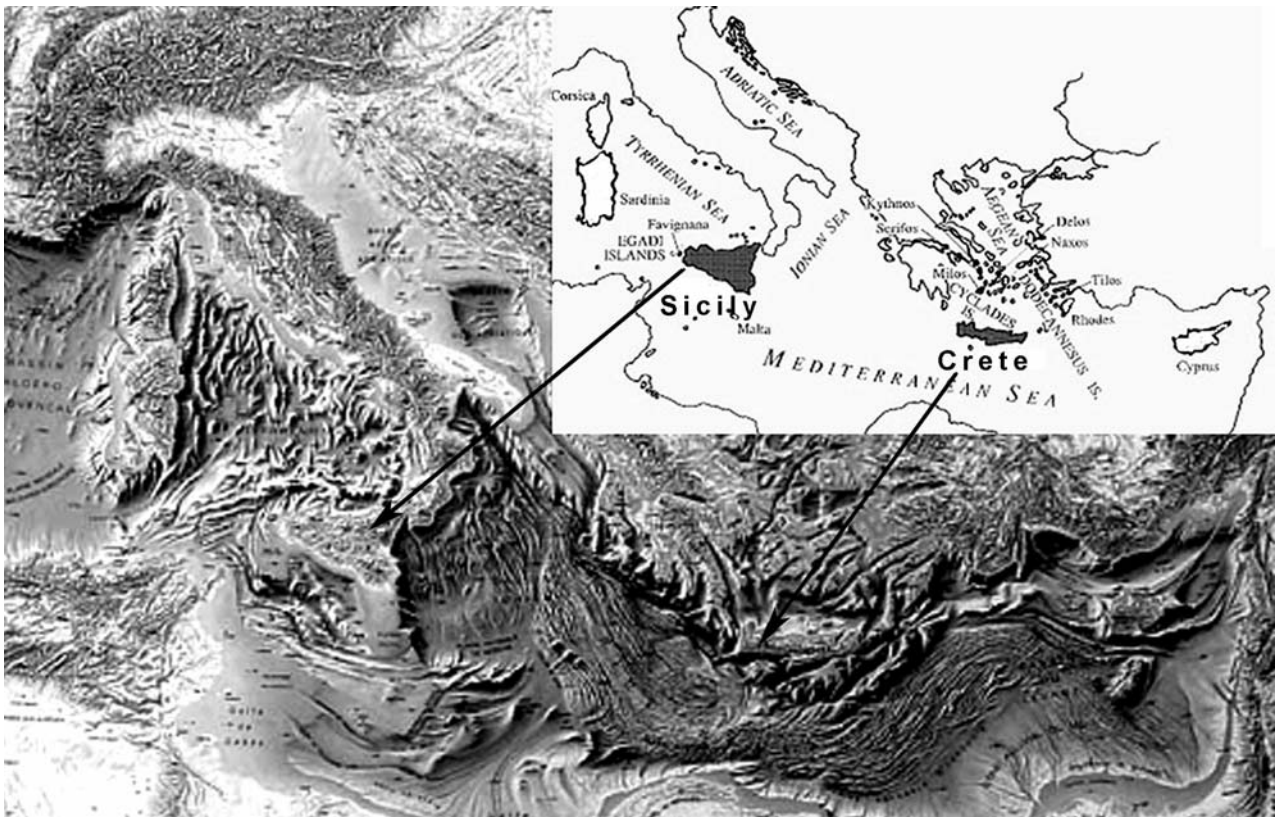

Figure 1 Map of the Mediterranean Sea.

tionary changes. These changes can be observed on islands of varying surface area, primary productivity and available resources, diversity and intensity of ecological interactions, and time and magnitude of isolation. Therefore, islands are regarded as living laboratories of evolution and an optimal context for the study of forces influencing evolution and diversification. Two main issues have been attentively scrutinized and debated: the loss of biodiversity and the peculiar changes undergone by island settlers, above all changes in body size of endemic vertebrates. This pattern was first described in insular mammals by Foster (1964) as a tendency for rodents (and possibly marsupials) to increase, and artiodactyls, carnivores, and possibly lagomorphs (rabbits and hares) to decrease in body size on islands, with insectivores showing no consistent trend (see e.g. Freudenthal 1972; Reumer 1980; Reumer & Obeli 1988; Fons *et al*. 1997; Fanfani 2000). Afterwards, this pattern was considered a rule by VanValen ("island rule," Van Valen 1973, p. 32), which postulates gigantism in smaller and dwarfism in larger species of insular mammals (see also Thaler 1973).

The rule has a number of exceptions and departures from the predictions, which can be found among both extinct and extant endemic mammals of differing body size, trophic habits and phylogenetic affinities (see e.g. Freudenthal 1972; Prothero & Sereno 1982; Ganem *et al*. 1995; Capasso Barbato & Petronio 1986; Nor 1996; Mills *et al*. 2004; Meiri *et al*. 2006). Nevertheless, the "island rule" continues to be a key topic in island biogeography. Over time, plenty of hypotheses have been formulated to explain the causal mechanisms of body size modification and the debate continues today, with a diversity of alternative explanations, which either confirm or reject this "rule" (see e.g. Marquet & Taper 1998; Lomolino & Weiser 2001; Clegg & Owens 2002; Palkovacs 2003; Gould & MacFadden 2004; Kõhler & Moyà-Solà 2004; Meiri *et al*. 2004, 2005a,b, 2008; Goltsman *et al*. 2005; Lomolino 2005; Jessop *et al*. 2006; Millen 2006; Lomolino *et al*. 2006; Raia & Meiri 2006; Palombo 2007a, and references therein).

The present paper aims to contribute to the debate by analyzing and comparing the body size structure of insular mammalian faunas with the structure of coeval mainland faunas. To test the generality and the underlying causal mechanisms of body size changes in extinct insular

Table 1 Main equations used to calculate body mass of insular and mainland species

Taxon	Variable	r^2	Y-intercept	slope	Reference
Insectivora	lower M1: maximal area	0.966	1.4461	1.8228	Legendre (1989)
Cercopithecinae	lower M1: maximal lenght	0.944	-0.8840	0.3210	Delson *et al*. (2000)
Rodentia	lower M1: maximal area	0.972	2.0875	1.7548	Legendre (1989)
Viverridae	lower M1: maximal area	0.910	1.8870	1.6552	Legendre (1989)
Mustelidae	lower M1: maximal area	0.910	1.8870	1.6552	Legendre (1989)
Canidae	lower M1: maximal area	0.977	2.0745	1.4922	Legendre & Roth (1988)
Ursidae	lower M1: maximal lenght	0.180	1.2600	0.4900	Van Valkenburgh (1990)
Hyaenidae	lower M1: maximal lenght	0.690	-2.2700	2.9700	Van Valkenburgh (1990)
Felidae	lower M1: maximal lenght	0.900	-2.1500	3.0500	Van Valkenburgh (1990)
Elephantidae	Height at shoulder	0.937	-4.0960	3.2039	Palombo & Giovinazzo (2005)
Rhinocerotidae	Upper M2: maximal width of the occlusal surface	0.994	1.3451	2.8871	Janis (1990)
Equidae	III metacarpal: minimal antero-posterior breadth of the distal articular surface	0.966	-4.313	3.0560	Alberdi *et al*. (1995)
Hippopotamidae	Upper M2: maximal width of the occlusal surface	0.993	1.3450	2.8870	Janis (1990)
Suidae	Lower M2: maximal legth of the occlusal surface	0.944	1.1300	3.2010	Janis (1990)
Small and medium-sized ruminants	Widht of the occipital condiles	0.839	-4.3710	3.2198	Giovinazzo *et al*. (2006)
Large bovids	Metacarpal: Maximal antero-posterior breadth of the proximal articular surface	0.940	1.0784	2.7928	Scott (1990)
Large cervids	Upper M2: maximal width of the occlusal surface	0.959	1.0730	3.2180	Janis (1990)

species, the most interesting islands are those from which endemic faunas of different taxonomical composition, structure and geological age have been reported. The Pleistocene faunas from Sicily and Crete (Fig. 1) are of particular interest because faunal complexes (FCs) that differ in biodiversity and body size structure are present on the same island at different times.

METHODS

To describe the body size structure of selected insular FCs, only the mammalian species have been considered. Body mass, the most useful quantifier of a species' adaptation as far as fossil species are concerned, is here considered a proxy of body size, according to Gingerich *et al*. (1982).

Body mass structures of the Sicilian and Cretan FCs have been compared with those of the coeval FCs from Italy and Greece, respectively (see Kostopoulos *et al*. 2007; Palombo 2007b, and references therein). Body mass was estimated by choosing the most appropriate allometric relationships for each taxon (Table 1). The rank-ordered distribution in mammalian complexes of average body mass of each species has been assessed, as in Valverde (1964), separating carnivores from non-carnivorous species, but

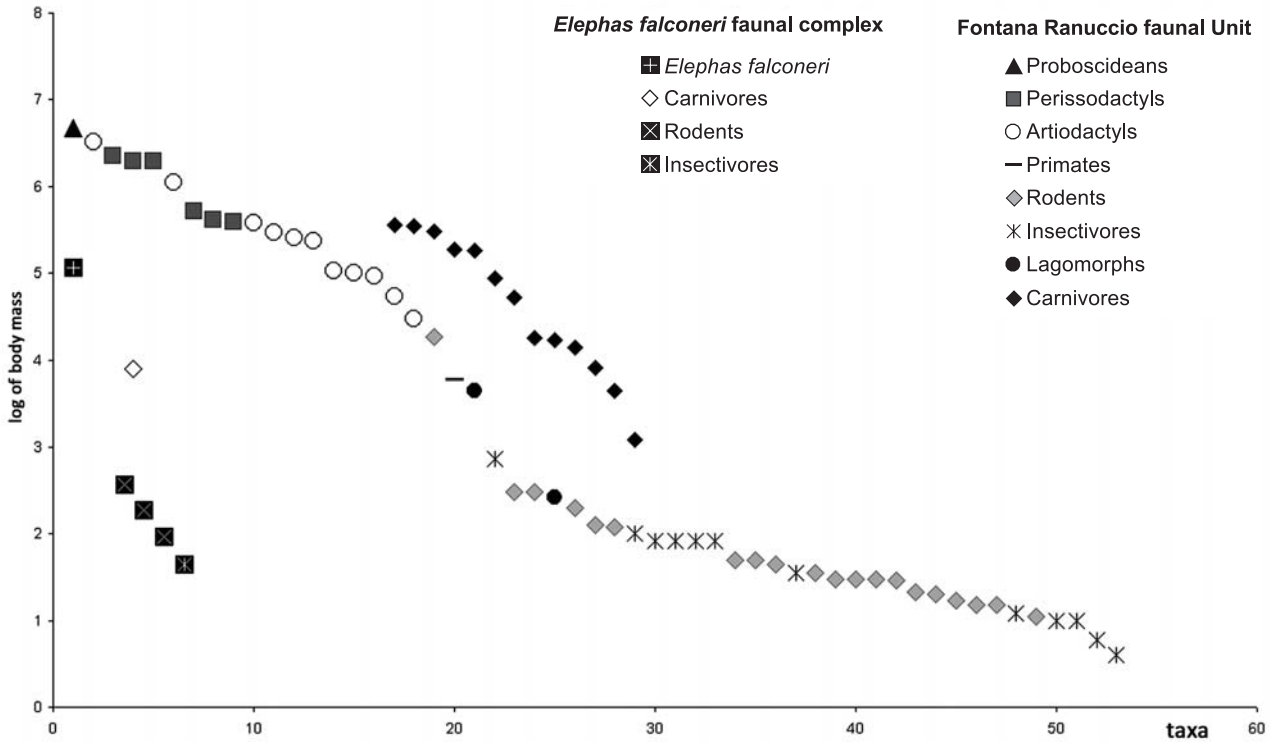

Figure 2 Comparison between the body size structure of the early Middle Pleistocene faunal complex from Sicily and the coeval mammalian complex from the Italian peninsula. For each faunal complex, each point corresponds to the mean body weight (on the y-axis) of a mammalian species, ordered by decreasing size (on the y-axis).

using the logarithm of body mass, as adopted in Legendre's cenograms (Legendre 1986, 1989).

Ecomorphological analyses have been used to establish the trophic habit of large mammal species and for assigning them to the various ecological categories, as in Palombo (2007b). The feeding behavior of herbivores has been inferred from the skull and mandible morphology, the hypsodonty index, the relative dimensions of premolar and molar rows, the mesowear and microwear patterns, the inclination of occipital bone and condyles etc. (see selected references in Palombo 2007b).

SICILY

The Middle to Late Pleistocene local faunal assemblages from Sicily can be arranged into four FCs: "*Elephas falconeri*" FC (early Middle Pleistocene), "*Elephas mnaidriensi"* FC (late Middle Pleistocene and Last Interglacial), San Teodoro Cave, Pianetti FC (early Last Glacial) and Castello FC (Pleniglacial-Lastest Glacial) (Bonfiglio *et al*. 2002; Masini *et al*. 2008, and references therein). Endemic taxa occur in the "*Elephas falconeri*" FC, "*Elephas mnaidriensis*" FC and San Teodoro cave-Pianetti FC, even though these FCs show, on average, a progressive increase in diversity and decrease in endemism. During the Last Glacial, the continental type faunal assemblages of the Castello FC demonstrate that faunal exchanges with the mainland had become easier, making Sicilian fauna very similar, but less diversified, to that of the southern Italian peninsula.

"Elephas falconeri" faunal complex

The "*Elephas falconeri*" FC (early Middle Pleistocene) is characterized by an unbalanced, very poorly-diversified and strongly endemic mammalian fauna, including small mammals that evolved from species already present in the Early Pleistocene Monte Pellegrino FC (*Leithia cartei*, *Leithia melitensis* and *Maltamys* sp. ex gr. *M. gollcheri-wiedincitensis*), as well as the descendent of newcomers, such as the shrew *Crocidura esui* (= *Crocidura sicula*, see Hutterer 1991), the otter *Nesolutra trinacriae* (= *Lutra trinacriae* in Masini *et al*. 2008) and *Elephas (Palaeoloxodon) falconeri*, the most dwarfed elephant so far discovered (Palombo 2001, 2007a). The presence of

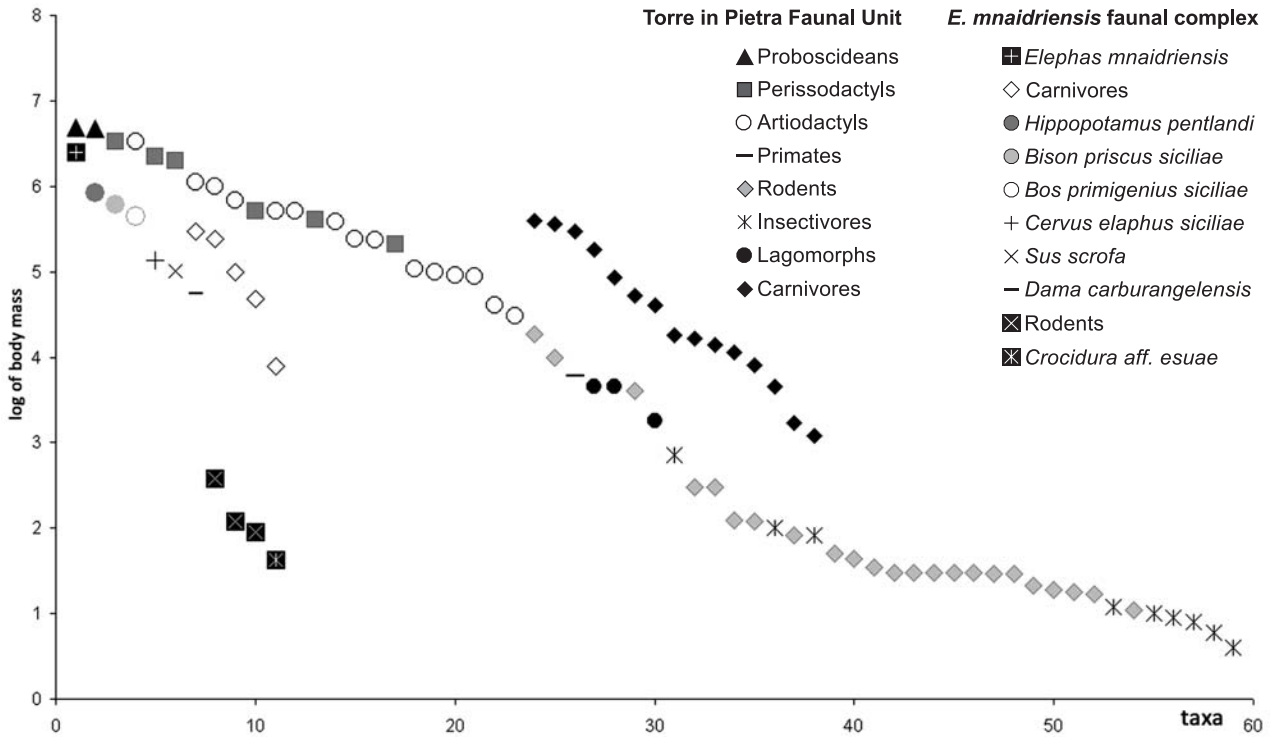

Figure 3 Comparison between the body size structure of the late Middle Pleistocene faunal complex from Sicily and the coeval mammalian complex from the Italian peninsula. For each faunal complex, each point corresponds to the mean body weight (on the y-axis) of a mammalian species, ordered by decreasing size (on the y-axis).

a small fox, *Vulpes* sp., and perhaps *Ursus* sp., needs to be confirmed. Paleontologic and geologic evidence denotes the occurrence of an insular system made up of geographically-isolated islands (the Hyblean Plateau, Peloritani and Nebrodi mountains), with no or only sporadic connections with the mainland (Bonfiglio *et al*. 2002).

The migration of founder settlers possibly took place during the Early Pleistocene/Middle Pleistocene transition, or slightly later, when, as a result of early Middle Pleistocene cold phases (MIS 24–22–?20), the sea level dropped and the distance between the island and mainland coastlines was reduced. The colonization by elephants occurred by chance over sea dispersal crossing a severe barrier, which prevented any other large mammals from reaching the island, whereas a "passive" arrival could be suggested for the small mammals.

A comparison between the body mass structure of this complex and that of the coeval FC of the Italian peninsula (Fontana Ranuccio faunal unit, FU, Palombo 2004, 2007b) (Fig. 2) clearly denotes the availability on the island of niches that on the mainland are typical of large and medium-sized herbivores (perissodactyls and artiodactyls), as well as of larger small mammals, such as leporids.

Elephas falconeri, a mixed feeder according to the microwear patter of its molars (Palombo, unpublished data) shifts toward the size, and niche, of the vacant mixed-feeder deer species, confirming the lack of any intra-guild competition. In addition, the lack of threatening predators implies the absence of selective predation pressure and inter-guild competition, so that *E. falconeri* could safely reduce its body mass toward the smallest size consistent with its body plan (Palombo 2007a).

Among endemic small mammals, the body size of the shrew is conspicuously larger than its mainland relative. In addition, it is worth noting that the body size of the small mammals of "*Elephas falconeri"* FC scales with a constant ratio roughly equal to a size ratio of 1.33 ˜ 2. This value matches the ratio considered by Hutchinson (1959) as permitting species to avoid competition, and partition resources with a minimum overlap (however, see Roth 1981; Maiorana 1990; Dayan & Simberloff 1998).

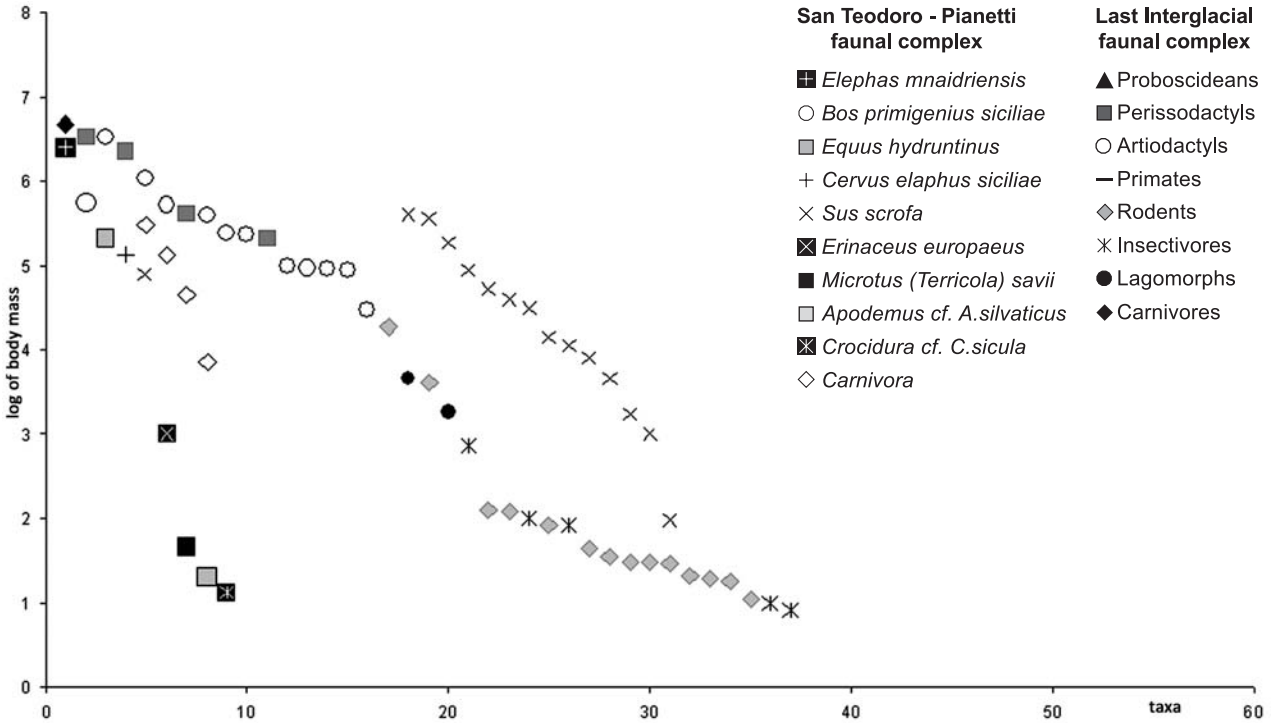

Figure 4 Comparison between the body size structure of the Last Interglacial faunal complex from Sicily and the coeval mammalian complex from the Italian peninsula. For each faunal complex, each point corresponds to the mean body weight (on the y-axis) of a mammalian species, ordered by decreasing size (on the y-axis).

"Elephas mnaidriensis" faunal complex

The late Middle to early Late Pleistocene "*Elephas mnaidriensis"* FC, ranging in age from approximately 250 to 80 ka (Bada *et al*. 1991; Bonfiglio *et al*. 1996; Rhodes 1996), is largely renewed as to the preceding "*Elephas falconeri"* FC. The fauna is impoverished, but quite diversified and balanced from a trophic point of view. The FC includes both endemic *(E. mnaidriensis*, *Hippopotamus pentlandi*, *Cervus elaphus siciliae*, *Dama carburangelensis*, *Bos primigenius siciliae, Bison priscus siciliae*) and mainland herbivores and carnivores (*Sus scrofa*, *Ursus* cf. *U. arctos, Canis lupus*, *Vulpes vulpes*) as well as top predators such as *Panthera spelaea* and *Crocuta crocuta*. Perissodactyls are still absent. A peculiarity of this fauna is the very low biodiversity of small mammals (*Crocidura* aff. *C. esui, Leithia* cf. *L. melitensis, Maltamys* sp. ex gr. *M. gollcheri-wiedincitensis*), which are represented by survivors from the *Elephas falconeri* FC.

The colonization giving rise to the "*Elephas mnaidriensis"* FC consisted of a set of migratory waves that probably took place during the sea level drop (Haq *et al*. 1987) related to the stadial oscillations in the late Middle Pleistocene (MIS 10, 8 and 6). These phases involved several large mammals, including some with limited swimming abilities, such as carnivores and bovids. As a result, the "*Elephas mnaidriensis"* FC represents a subset of the more diversified mainland community, but it is rather varied in terms of trophism and intraguild diversification. Remains of the most prominent endemic species of this FC, *Elephas (Palaeoloxodon) mnaidriensis,* have been retrieved from several localities, frequently associated with endemic, but not truly dwarfed artiodactyls, as well as with continental taxa such as large carnivores and suids. Endemic artiodactyls are moderately modified compared with the cogeneric or cospecific taxa from the mainland (approximately 20% for the red deer), but the endemic nature of the fauna is apparent mainly from the reduction in size of these taxa. All in all, the composition of large mammal fauna, roughly similar to that found in the southern Italian peninsula, and the moderate endemization suggest that temporary connections with southern Italy occurred (Bonfiglio *et al*. 2002, Mangano 2007). The fauna points to a certain degree of isolation, explained as a territory not reachable from the mainland for all taxa and it seems that

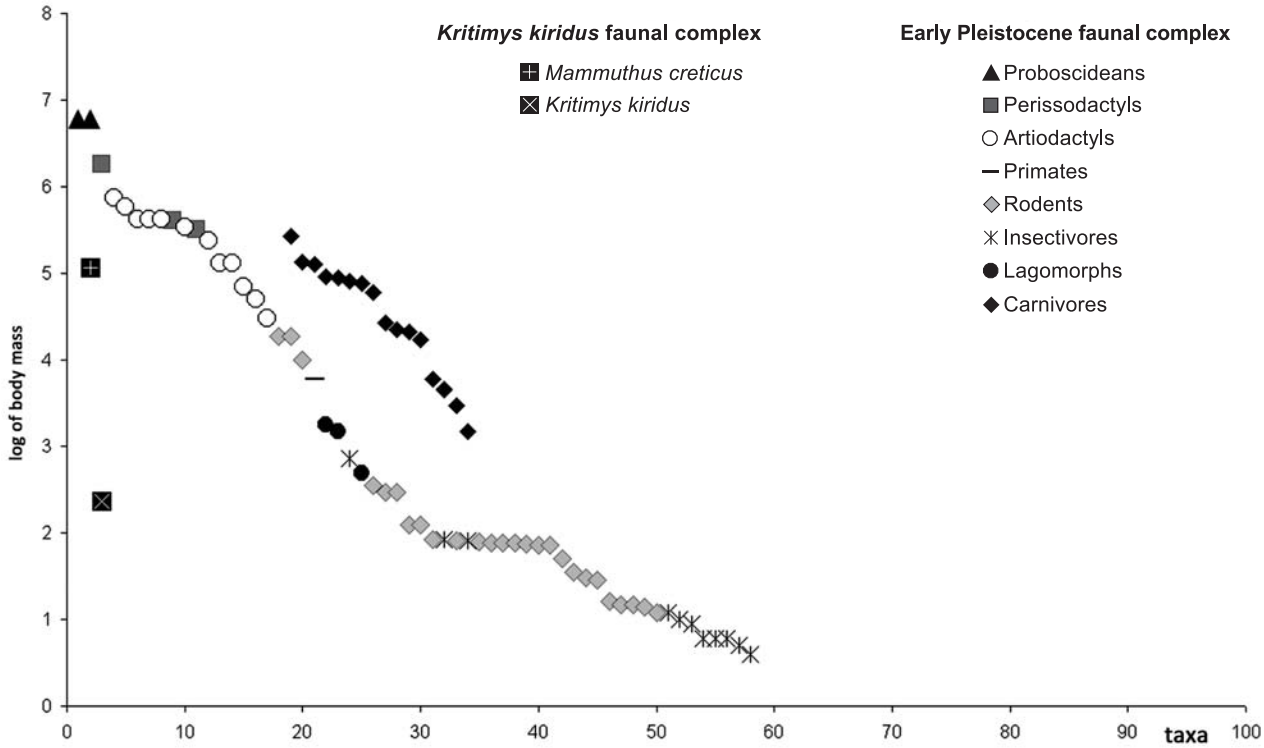

Figure 5 Comparison between the body size structure of the Early Pleistocene faunal complex from Crete and the coeval mammalian complex from the Greek mainland. For each faunal complex, each point corresponds to the mean body weight (on the y-axis) of a mammalian species, ordered by decreasing size (on the y-axis).

filtering barriers, possibly ecological in nature, affected the dispersal, preventing small mammal from reaching Sicily.

A comparison between the body mass structure of late Middle Pleistocene FCs from Sicily and the Italian peninsula (Torre in Pietra FU, Palombo 2004, 2007b) (Fig. 3) demonstrates that larger middle-sized herbivores (mixed feeder deer) only slightly reduced their size on the island. However, larger herbivores (grazer bovids) shifted into the niche occupied on the mainland by grazers, such as middle-sized horses, whereas the endemic hippopotamus *H. pentlandi*, likely a grazer, and the elephant *E. mnaidriensis*, a mixed-feeder, respectively, entered the niches typical of mainland large horses (grazers) and rhinoceroses (mixed feeders) vacant on the island. Conversely, no significant change in body size occurred for large and medium-sized carnivores, coherently with the relatively unchanged size of the most preferred prey.

San Teodoro-Cave Pianetti faunal complex

The San Teodoro-Cave Pianetti FC, dating to the early Last Glacial, is characterized by the persistence of *E. mnaidriensis*, by the dispersal of equids (*Equus hydruntinus*) and of mainland small mammals. The new small mammals that substituted those of the previous FCs, are represented by taxa still present in Sicily [*Microtus* (*Terricola*) *savii*, *Crocidura* cf. *C. sicula*, *Apodemus* cf. *A. sylvaticus*, *Erinaceus europaeus*] as well as in the balanced fauna belonging to the Sicilian latest Pleistocene Castello FC, where no insular taxa are present. Conversely, the turnover of large mammals does not seem to be important because nearly all of the large mammals belonging to San Teodoro-Cave Pianetti FC were likely inherited from "*Elephas mnaidriensis"* FC, with the exception of *N. trinacriae* and *H. pentlandi*, which were no longer recorded. However, new migrations of mainland relatives of the large mammals belonging to San Teodoro-Cave Pianetti FC, cannot be entirely ruled out because the arrival of taxa such as the ground vole, which has a fossorial lifestyle, and the small horse, a typical dweller of open landscapes, might imply the existence of temporary land bridges related to pronounced eustatic lowstand of sea level. This period coincides with the lowest sea level since

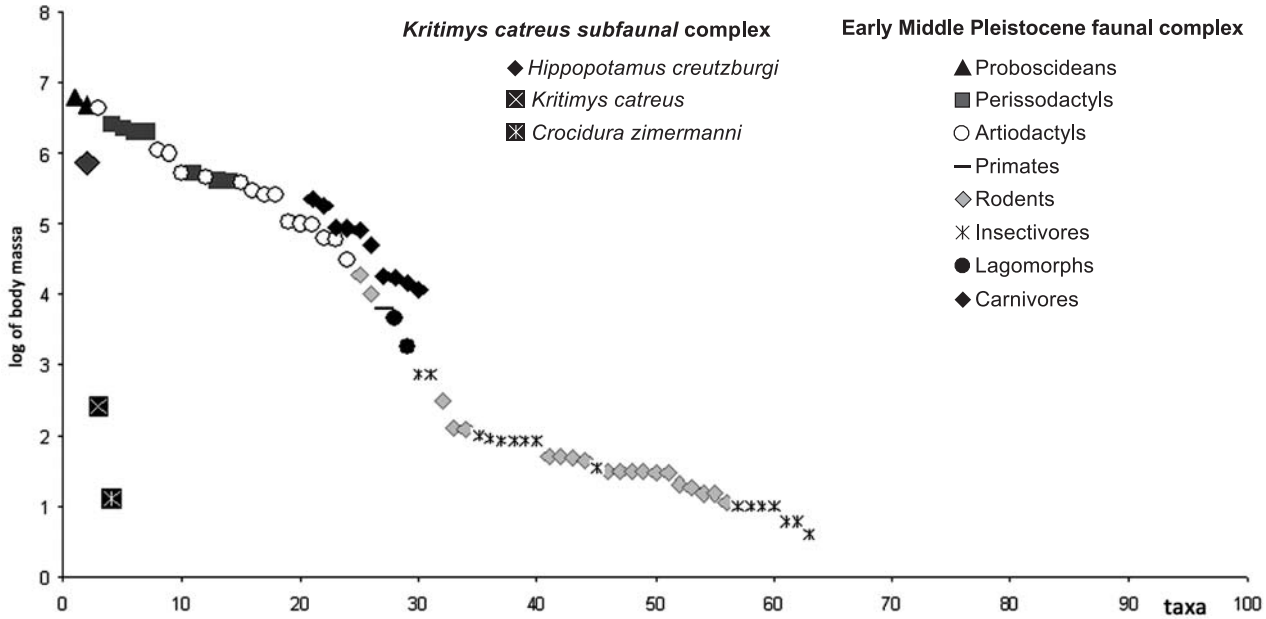

Figure 6 Comparison between the body size structure of the early Middle Pleistocene faunal complex from Crete and the coeval mammalian complex from the Greek mainland. For each faunal complex, each point corresponds to the mean body weight (on the y-axis) of a mammalian species, ordered by decreasing size (on the y-axis).

the Miocene (Haq *et al*. 1987), so pronounced climatic negative oscillations could have lead to more than one episode of "traffic light" dispersals (sensu Vrba 2005). The idea that it was much easier to reach the island since the times of San Teodoro-Cave Pianetti FC, is only partially confirmed by the taxonomical composition of the following Castello FC (*Mustela* cfr. *M. nivalis, Martes* sp., *Ursus arctos*, *Canis lupus*, *Vulpes vulpes*, *Lynx lynx, Sus scrofa*, *Equus hydruntinus*, ?*Equus ferus, Cervus elaphus*, *Bos primigenius*), in which almost all local ungulates were replaced by normal sized mainland taxa, but the herbivore diversity is lower than that of San Teodoro-Cave Pianetti FC. Either sampling and taphonomic biases or the reduced biodiversity of southern-most western Italy (Bonfiglio *et al*. 2002) during the Last Glacial might be responsible for deficiencies of the faunal list of the Castello FC.

A comparison between the body mass structure of the San Teodoro-Cave Pianetti FC and that of the Italian peninsula during the MIS 5 (Fig. 4) demonstrates that elephants, as well large and middle-sized herbivores, only slightly reduced their size, whereas the size of carnivores apparently did not change. The pattern of body mass changes shown by herbivores implies the shift towards the size of mainland species of similar trophic behavior that are vacant on the island, as already pointed out for the "*Elephas mnaidriensis"* FC.

Remarks on Pleistocene Sicilian faunal complexes

The body mass structure of the Middle and Late Pleistocene Sicilian FCs seems to confirm the general nature of the "island rule," but it underlines the relationship between the changes of size of endemic ungulates and the intra-guild shift towards the size of species that are vacant on the island: Sicilian ungulates changed their size according to the availability for insular species of niches that on the mainland are typical of medium-sized and large herbivores with similar trophic behavior (Caloi & Palombo 1995; Palombo 2007b; unpublished data). The absence of predator pressure was less important even though the lack of any large predator most likely drove *E. falconeri* to reach their minimal size. In addition, the hypothesis that the insular area might have consistently affected the degree of size reduction of insular settlers is not supported because during the early Middle Pleistocene *E. falconeri* inhabited territories that were just a little smaller than those settled by *E. mnaidriensis* of the late Middle Pleistocene. Indeed, during the early Middle Pleistocene, Sicily's shape was roughly similar to its present shape, even if some

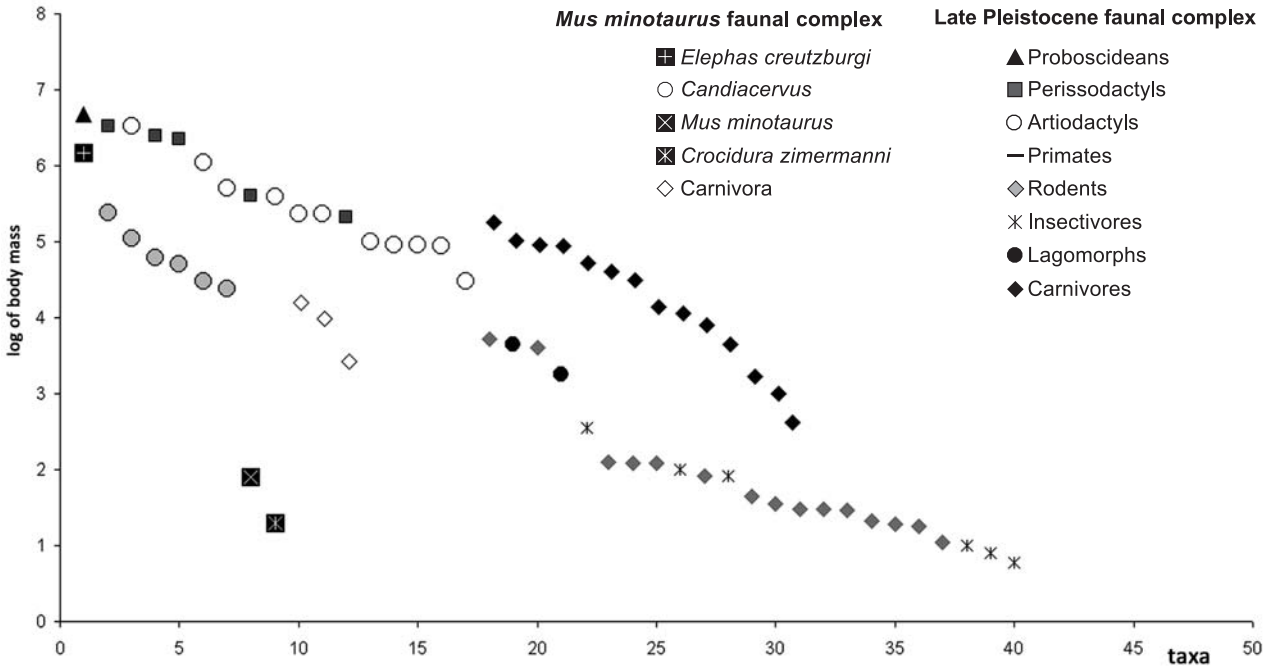

Figure 7 Comparison between the body size structure of the Late Pleistocene faunal complex from Crete and the coeval mammalian complex from the Greek mainland. For each faunal complex, each point corresponds to the mean body weight (on the y-axis) of a mammalian species, ordered by decreasing size (on the y-axis).

territories were still below the sea (Agnesi *et al*. 1998). Sicily was already quite a large island and its productivity was likely enough to support a mammalian fauna more diversified than that of the "*Elephas falconeri"* FC.

CRETE

The biochronological setting of the Cretan Pleistocene mammalian fauna is based on the phylogeny of endemic murids: Mayhew (1996) distinguished five biozones based on the two endemic genera, the larger *Kritimys* and the smaller *Mus* murids. Taking into account the large mammals, two main FCs can be distinguished: the strongly impoverished *Kritimys* FC (including *Kritimys* aff. *K. kiridus*, *Kritimys kiridus* and *Kritimys catreus* subcomplexes [sFC]), and the strongly unbalanced but more diversified *Mus* FC (including the *Mus bateae* and *Mus minotaurus* sFC) (de Vos 1984, 1996, and references therein; Palombo 2007a). *Mammuthus creticus* and *Hippopotamus creutzburgi* are the only large mammals in the *Kritimys* FC, whereas larger elephants occur in the *Mus minotaurus* sFC, together with at least six endemic deer, which can be regarded as an outstanding example of adaptive radiation (de Vos 1984, 1996, 2000; Caloi & Palombo 1995; Palombo *et al*. 2008 and references therein).

The FCs thus far described for Crete denote the difficulty of colonization permitting only a few species to reach the island, and testify the persistence of unbalanced and impoverished faunas, though an evolution towards a slightly more diversified fauna is detectable. Moreover, the taxonomical composition shown by Cretan FCs poses some questions mainly related to the time of the migrations and the coexistence of hippopotamuses and elephants. For instance, although the occurrence of a dwarfed hippopotamus in the *Kritimys* FC (suggested by Spaan (1996) on the basis of ribs found at Siteia I (a locality where *K.* aff. *kiridus* also occurs) needs to be confirmed, it is difficult to justify the absence of elephant settlers at the time of *Kritimys catreus* and *Mus bateae* sFC. On the basis of available data, it seems that Akrotiri Melekas Cave 1 is the only site where *M. creticus* remains have been found (Lax 1996; Mol *et al*. 1996; Poulakakis *et al*. 2002) and thus far the dwarfed mammoth has never been found in *K. catreus* or *Mus bateae* sFC. *Hippopotamus creutzburgi* is not reported from the *Kritimys kiridus* sFC (Poulakakis *et al*. 2006). However, Sondaar and Van der Geer (2005, p. 11) state that the "youngest association of *E. creticus* with *H. creutzburgi* is Katharo 1 (absolutely dated (AAR and ESR) around 400,000 years". In fact, the

Katharo basin scanty elephant remains (an almost completely developed right M2 and one fragment of tusk comparable in size to the mainland *E. antiquus*) have been recovered from sandy deposits that probably overlay the clay deposits from which *H. creutzburgi* remains were retrieved (see Poulakakis *et al*. 2002). Accordingly, *M. creticus* might be older than *H. creuztburgi* and the coexistence of these taxa is doubtful. More data and further studies are certainly required to clarify this important issue, and to provide evidence for a better understanding of body size trends in endemic mammals from Crete.

Herein only the body mass structure of the better known *K. kiridus*, *K.catreus* and *Mus minotaurus* sFC have been analyzed.

Kritimys faunal complex

In the *Kritimys* FC, three different evolutionary stages of this quite large endemic murid can be recognized (*Kritimys* aff. *kiridus, K. kiridus* and *K. catreus*) that likely developed during the Early Pleistocene (Mayhew 1977, 1996). *Kritimys* aff. *kiridus* has been reported from Siteia (= Sitia) 1, whereas remains of the dwarfed elephant *Mammuthus creticus* have been found associated with *K. catreus* in the somewhat more recent (likely Early Pleistocene) locality of Cape Meleka 1 (Mayhew 1996).

The fauna is strongly unbalanced and impoverished because just two species, the dwarfed mammoth and the murid, are unquestionably thus far recorded. *M. creticus* is a taxon based on nine partial molars, a fragment of an incisor and a fragment of a vertebra, collected by Miss Bate in 1904 from a cave now known as Akrotiri Melekas Cave 1 (Bate 1907). A molar with an attached *K. kiridus* mandible was later collected by Paul Sondaar in 1973 (Mol *et al*. 1996). Thereby, the body size of this species can only be inferred on the basis of comparison with other Mediterranean endemic elephants, such as *Elephas (Palaeoloxodon) falconeri* from Spinagallo Cave (Sicily, Ambrosetti 1968; Palombo unpublished data), whose teeth are on average smaller, and *Elephas (Palaeoloxodon) tiliensis* from Tilos, slightly larger (Theodorou 1983; Theodorou *et al*. 2007).

The comparison between the body mass structure of this complex and the coeval Middle Pleistocene Greek fauna (Fig. 5) clearly denotes the shift in size of *M. creticus* towards the size of large herbivores that are vacant on the island. The Cretan mammoth did not reach the same reduction in size as undergone by the Sicilian *E. falconeri*, although the presence of a possible competitor, *H. creutzburgi*, at that time (a rib is reported by Spaan, 1996 from Siteia) needs to be confirmed.

Hippopotamus creutzburgi is known from a number of sites in the Katharo basin (possibly early Middle Pleistocene in age, from approximately 0.8 to 0.4 Ma, Rees *et al*. 1996), as well from several caves, some of which (e.g. Stavros cave) also yield *K. catreus* and *Crocidura* remains.

A comparison between the body mass structure of *K. catreus* sFC and the early Middle Pleistocene mainland fauna (Fig. 6) shows that the average size of *H. creutzburgi*, considerably smaller than its mainland ancestor, shifts towards the size of large herbivores that are vacant on the island. However, *H. creutzburgi* is slightly smaller than *M. creticus*, and definitely larger than the endemic Cypriotic hippopotamus *Phanourios minor* (Boekschoten & Sondaar 1972), although no competitors are apparently present on Crete at that time. Remains of Cretan hippopotamus from different localities show variation in size that induced Kuss (1970) to distinguish two subspecies: *H. creutzburgi creutzburgi* and *H. creutzburgi parvus*; however, the variation in size would not be too large for one species (Spaan 1996). Therefore, whether the variations are the result of fluctuation in ecological factors that could have any evolutionary implication, however, remains an unanswered question.

Mus faunal complex

The *Mus* FC possibly developed during the late Middle and Late Pleistocene. The oldest record of *Mus* is reported from the Stavros Micro site; the lowest stratigraphic occurrence of *Candiacervus* is in Charoumbes 2, and *Elephas* and *Candiacervus* are reported together for the first time at Charoumbes 3 (Sondaar & van der Geer 2005).

At least six endemic deer are the most typical taxa of this FC (de Vos 1984, 1996, 2000; Capasso Barbato 1992; Capasso Barbato & Petronio 1986; Palombo *et al*. 2008). Their forerunners reached the island, probably by swimming, during the latest Middle Pleistocene glacio-eustatic sea lowering. When deer arrived on the island, no direct competitors were present and, consequently, numerous habitats and niches were likely available (de Vos 1996, 2000; Palombo 1996). This allowed their adaptive radiation and the differentiation of species varying in size, feeding behavior and locomotion: *Candiacervus ropalophorus*, with a withers height of approximately 40 cm; *Candiacervus* spp. II approximately 50 cm high; *Candiacevus cretensis* approximately 65 cm high; *Candiacervus rethymnensis*, whose size is comparable to the mainland species *Cervus elaphus*; the larger *Candiacervus dorothensis*; and the giant *Candiacervus major*. Together with deer, a quite large elephant and some small mammals (*Crocidura zimermanni, Mus minotaurus*),

as well as small Carvivora (?*Martes foina*, ?*Meles meles*, *Lutrogale cretensis*), were present. The taxonomic status of the endemic elephants of *Mus* FC is still a debated issue (cfr. Mol *et al*. 1996; Symeonidis *et al*, 2000; Poulakakis *et al*. 2002; Palombo 2007a, and references therein). On the basis of the evidence available, the majority of the remains can be ascribed to *Elephas creutzburgi*, whose size was on average approximately 70% the size of *Elephas (Palaeoloxodon) antiquus* specimens from the Middle Pleistocene of the Greek mainland (Tsoukala & Lister 1998; Palombo, unpublished data). Specimens slightly smaller than or of approximately the same size as the mainland *Elephas antiquus* have also been reported in *Mus minotaurus* sFC. Whether such specimens belong to a third taxon or could be ascribed to the mainland *E. antiquus* has been extensively debated (see Mol *et al*. 1996; Symeonidis *et al.* 2000; Poulakakis *et al*. 2002; Palombo 2007a). The possibility of occasional migration of a single individual from the mainland or the difficulty of maintaining a genetic flow between insular and continental populations also, although unlikely, cannot entirely be discarded.

A comparison between the body mass structure of the *Mus* FC and that of Greek Late Pleistocene FC (Fig. 4) demonstrates that elephants only slightly reduced their size, whereas the body mass of deer matches those of large as well medium-sized mainland herbivores with similar trophic behavior (Caloi & Palombo 1995, 1996). The body size of the small endemic mammals is larger than that of their mainland relatives.

Remarks on Pleistocene cretan faunal complexes

The structure of the Cretan FCs (Figs 5,6), the size reduction of largest mammals (*M. creticus* and *H. creutzburgi*), as well as the radiation of deer, is consistent with the availability of the island niches that on the mainland are typical of large and medium-sized herbivores (perissodactyls and artiodactyls). Besides, it is worth noting that the body size of endemic small mammals, *Mus* and *Crocidura*, progressively increased after the disappearance of the lager *Kritimys* species. Taking into account that the hippopotamus seems to have reduced its size less than expected according to the available niches (its average body mass reduction is definitely less than the reduction undergone by the Cypriotic *Phanourios minor*), the occurrence of more than one population of hippopotamuses, differing, and scaling in size, cannot be completely ruled out (see Spaan 1996 and references therein for a discussion).

DISCUSSION

In the past decades, several authors have emphasized the role played by different factors to explain evolutionary patterns in isolated areas, focusing at times on the reduced (often absent) predation pressure exerted by large carnivores, the host-island surface, trophic requirements and metabolic rate, population density and overcrowding or overgrazing, genetic segregation and endogamy, phylogenetic inertia and species intrinsic properties, dispersal ability and isolation (see Palombo 2007a, and references therein).

More recent views have focused on: (i) reduced insular species richness leading to rarity of predators and competitors; (ii) selective advantage of body size alteration via life-history traits; (iii) existence of an "optimal" or "fundamental" body size (for a particular body plan and ecological strategy) to which body size of insular species tends to converge (see Palkovacs 2003; Lomolino 2005; Lomolino *et al*. 2006; Meiri *et al*. 2006; Raia & Meiri 2006; Palombo 2007a, and references in those papers).

These hypotheses are not mutually exclusive, and patterns shown by particular species (sometimes varying with biotic and abiotic characteristics of the islands) highlight the synergetic influences of several factors as well as the different underlying mechanisms affecting body size in carnivorous and non-carnivorous species.

Comparison of body mass structures of insular and mainland Pleistocene mammalian communities of the Mediterranean region suggests that, among herbivores, the most dwarfed taxa occurred in faunas where no other large herbivores lived, whereas the largest taxa appeared in more diversified faunas, which might include predators. Moreover, size changes of endemic taxa contradict any relationship between the magnitude of body-size shifts and the island surface. Indeed, endemic taxa originating from successive migrations by the same continental taxon on the same island, such as the endemic Sicilian elephants, show remarkably different reduction in size, despite the unnoticeable differences in island surface over time.

Results obtained stress that the dwarfing in herbivores is more related to presence/absence of species competing for resources than of predators. This is particularly true for the largest species in quite diversified faunas of different geographic regions, such as *E. mnaidriensis* from Sicily and *E. creutzburgi* from Crete that share a similar, not remarkable, size reduction even if only the Sicilian fauna included large carnivores. It is to be expected that the extent of size decrease is also affected by varying predation pressure, for instance, the absence of both predator

and competitor pressure likely contributed to drive *E. falconeri* to reach a minimal size.

Sicilian and Cretan endemic deer are of special interest, because their modifications enable us to compare different patterns assessing the influence of various factors (biodiversity and structure of insular communities and type and availability of niches, which on the mainland are peculiar of possible deer competitors) on size changes of insular ungulates. When the forerunners of Cretan deer arrived on the island, neither direct competitors nor predators were present. Thus, Cretan deer had the possibility of colonizing very different niches, and the radiative evolutionary process led to species scaling in body size. Indeed, differences in body size promote mammal coexistence, permitting species to avoid competition, and to partition resources with a minimum overlap. Conversely, the size reduction of the Sicilian deer, *D. carburangelensis* and *C. elaphus siciliae*, was not remarkable because in the *E. mnaidriensis* FC, the body size distribution of medium-sized herbivores roughly matches that characterizing coeval mainland communities.

All in all, the analysis of the structure of Pleistocene insular communities from Sicily and Crete suggests that in unbalanced insular communities, changes in size of non-carnivorous mammals largely depends on the altered intra-guild competition and on the nature of species, which are vacant on the island.

It is well known that interspecific competition via coevolution (which in turn could generate geographical variation) prevents the coexistence of species with overlapping body sizes (see Brown & Wilson 1956; Schoener 1989; Dayan & Simberloff 1998 and references therein), thereby on an "ideal" mainland, community niches would scale in a predictable way. As only a few species of mainland community can migrate to islands, because of the filtering effect of the barrier that insular settlers have to cross, insular faunas are generally less diversified than the coeval faunas on the mainland, and the niches of vacant species became available for new comers. As a result, body size of insular species shifts towards the size of mainland species of comparable trophic habits that are vacant on islands and the size scaling in insular fauna should notably increase.

Mammals derive some advantages from changing their size. Larger-sized mammals generally require more food, and need larger home ranges. Reducing their size, large herbivores increase the opportunity to exploit the environment and optimize energy costs. Moreover, the changed metabolic rate might enhance/reduce the reproductive rate in large/small mammals (see Mappes *et al*. 2008 for a discussion). The dwarfed species *E. falconeri* is supposed to be selected to have given birth after a progressively shorter pregnancy period and at a lower body weight than its mainland ancestors (Raia *et al*. 2003). In this case, the hypothesis that the body size reduction and increasing metabolic rate lead large mammals to a higher reproduction rate cannot be completely ruled out. This, in turn, might allow population size to grow rapidly and the critical minimum number of specimens required to be attained to avoid the threat of extinction caused by low density of a pioneer population (Palombo 2007a).

Accordingly, we can suppose that, given the intrinsic characteristics connected with their body plan, and removing biotic and abiotic environmental constraints, the body size of insular species could converge towards the size allowing the best energetic equilibrium. Evolutionary trends in endemic taxa also involve occupying or creating novel niches, possibly producing morphologies different from those of their ancestral forms.

CONCLUSION

The results obtained provide evidence that: (i) size of endemic species is not directly dependent on the area of islands; (ii) evolution and size of endemic species might be indirectly affected by isolation (constraining colonization from the mainland) and physiography (sometimes permitting adaptive radiation); (iii) in unbalanced insular communities, the shift in size of non-carnivorous species largely depends on the nature of vacant species; and (iv) body size of carnivorous species mainly depends on the size of the most available prey. Consequently, we maintain that the body size of non-carnivorous insular species mainly results from the peculiar biological interactions that characterize unbalanced, impoverished insular communities. On the mainland, in an "ideal" community, niches scale in a predictable way, but just a few species from these communities can cross a severe barrier to enter islands. Therefore, the ecological structure of communities might be rebuilt, and newcomers on islands might develop new adaptations that depend on the nature, and size, of vacant species. Accordingly, ecological interaction is a major driver behind the evolution in unbalanced insular communities, allowing the optimization of the energy balance by means of changes in size. Removing biotic and abiotic environmental constraints, the body size of non-carnivorous insular species could converge towards a taxon-specific "critical size" depending on the intrinsic characteristics connected with their body plan. Conversely, body size of carnivorous species mainly depends on the size of the most available prey as well as on

the adaptive strategy for a more efficient energy use under the special environmental conditions of insular ecosystems.

Size changes undergone by insular herbivores are an ecological (and evolutionary) response of different non-carnivorous lineages to competition pressures that vary over space and time, giving rise to different size change even in a single clade. However, these changes are a complex phenomenon and the significance of some exceptions cannot be neglected. Further study is certainly required to provide evidence for the causal mechanism driving the body-size evolution of insular vertebrates.

ACKNOWLEDGMENTS

I thank colleagues and people of the following museums and institutions I visited for granting me access to the material in their care and for their help: Instituut Voor Aardwetenschappen, Utrecht; Natural History Museum, London; Naturhistorisches Museum, Basel; Institut de Paleontologie Humaine, Paris; Museo Nacional de Ciencias Naturales, Madrid; Aristotle University of Thessaloniki; Museo di Geologia e Paleontologia, Florence; Museo di Paleontologia, Cagliari; Museo di Paleontologia, Rome; Museo Gemellaro, Palermo.

I thank the two anonymous reviewers for their comments that improved the quality of the paper.

Research was supported by a MIUR 60% grant 2006 to M. R. Palombo.

REFERENCES

Agnesi V, Macaluso T, Masini F (1998). L'ambiente e il clima della Sicilia nell'ultimo milione di anni. *Prima Sicilia, alle origini della società siciliana* **1**, 31–45.

Ambrosetti P (1968). The Pleistocene Dwarf Elephants of Spinagallo (Siracusa, South-Eastern Sicily). *Geologica Romana* **7**, 277–397.

Bada JL, Belluomini G, Bonfiglio L, Branca M, Burgio E, Delitala L (1991). Isoleucine epimerization ages of Quaternary Mammals of Sicily. *Il Quaternario* **4**, 5–11.

Bate DMA (1907). On elephant remains from Crete, with description of *Elephas creticus* sp.n. *Proceedings of the Zoological Society London* **2**, 238–50.

Boekschoten GJ, Sondaar PY (1972). On the fossil mammalia of Cyprus. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* Series B, **75**, 306–38.

Bonfiglio L, Di Geronimo S, Insacco G, Marra AC (1996). Large mammal remains from Late Middle Pleistocene deposits of Sicily: new stratigraphic evidence from the western edge of the Hyblean Plateau (Southeastern Sicily). *Rivista Italiana di Paleontologia e Stratigrafia* **102**, 375–84.

Bonfiglio L, Mangano G, Marra AC, Masini F, Pavia M, Petruso D (2002). Pleistocene Calabrian and Sicilian bioprovinces. *Geobios,* Mem spec. **24**, 29–39.

Brown WL, Wilson EO (1956). Character displacement. *Systematic Zoology* **5**, 49–64.

Caloi L, Palombo MR (1995). Functional aspects and ecological implications in Pleistocene endemic cervids of Sardinia, Sicily and Crete. *Geobios* **28**, 247–58.

Caloi L, Palombo MR (1996). Functional aspects and ecological implications in Hippopotami and Cervids of Crete. In: Reese DS, ed. *Pleistocene and Holocene Fauna of Crete and its First Settlers*. *Monography in World Archaeology* **28**, 125–52.

Capasso Barbato L (1992). Nuova specie di cervide del Pleistocene di Creta. *Atti Accademia Nazionale dei Lincei, Memorie Classe di Scienze Fisiche Matematiche e Naturali* **9**, 187–220.

Capasso Barbato L, Petronio C (1986). *Cervus major* n. sp. of Bate cave (Rethymnon, Crete). *Atti Accademia Nazionale dei Lincei, Memorie Classe di Scienze Fisiche Matematiche e Naturali* **8**, 59–100.

Clegg SM, Owens IPF (2002). The "island rule" in birds: medium body size and its ecological explanation. *Proceedings Royal Society London*, B. **269**, 1359–65.

Dayan T, Simberloff D (1998). Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. *Mammal Review* **28**, 99–124.

de Vos J (1984). The endemic Pleistocene deer of Crete. *Verhandelingen des Koninklijke Nederlandsevan Wetenschappen, Afdeling Natuurkunde, Erste Reeks* **31**, 1–100.

de Vos J (1996). Taxonomy, ancestry, and speciation of the endemic Pleistocene deer of Crete compared with the taxonomy, ancestry, and speciation of Darwin's finches. In: Reese DS, ed. *Pleistocene and Holocene Fauna of Crete and its first Settlers*. *Monography in World Archaeology* **28**, 99–110.

de Vos J (2000). Pleistocene deer fauna in Crete: Its adaptive radiatins and extinction. *Tropics* **10**, 125–34.

Delson E, Terranova CJ, Jungers WL, Sargis EJ, Jablonski NG, Dechow PC (2000). Body mass in Cercopithecidae (primates, mammalia), estimation and scaling in estimation and scaling in extinct and extant taxa. *American Museum of Natural History, Antropological Papers* **83**, 1–159.

Fanfani F (2000). Revisione degli insettivori (Mammalia) tardo neogenici e quaternari dell'Italia peninsulare (PhD thesis). Università di Modena and Reggio Emilia, Modena, 283.

Fons R, Poitevin F, Catalan J, Croset H (1997). Decrease in litter size in the shrew *Crocidura suaveolens* (mammalia, insectivora) from Corsica (France), evolutionary response to insularity? *Canadian Journal of Zoology* **75**, 954–8.

Foster JB (1964). Evolution of mammals on islands. *Nature* **20**, 234–5.

Freudenthal M (1972). *Deinogalerix koenigswaldi* nov. gen., nov. spec., a giant insectivore from the Neogene of Italy. *Scripta geologica* **14**, 1–19.

Ganem G, Granjon L, Ba K, Duplantier J M (1995). Body size variability and water balance: a comparison between mainland and island populations of *Mastomys huberti* (Rodentia: Muridae) in Senegal. *Experientia* **51**, 402–10.

Gingerich PD, Smith BH, Rosenberg K (1982). Allometric scaling in the dentition of primates and prediction of body weight from tooth size in fossils. *American Journal of Physical Anthropology* **58**, 81–100.

Giovinazzo C, Altamura S, Palombo MR (2006). Determinazione della massa corporea nei ruminanti di media e piccolo taglia: un nuovo approccio metodologico. In: Fonda G, Melis R, Romano R, eds. *Abstracts Giornate Paleontologia 2006, Trieste 8–10 giugno*, 39.

Goltsman M, Kruchenkova EP, Sergeev S, Volodin I, Macdonald DW (2005). 'Island syndrome' in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island. *Journal of Zoology* **267**, 405–13.

Gould GC, MacFadden BJ (2004). Gigantism, dwarfism, and Cope's Rule, 'Nothing in evolution makes sense without a phylogeny'. *Bulletin of the American Museum of Natural History* **285**, 219–37.

Haq BU, Hardenbol J, Vail PR (1987). Chronology of fluctuating sea levels since the Triassic. *Science* **235**, 1156–67.

Hutchinson GE (1959). Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* **93**, 145–59.

Hutterer R. (1991). Variation and evolution of the Sicilian shrew: taxonomic conclusions and description of a possibly related species from the Pleistocene of Morocco (Mammalia: Soricidae). *Bonner Zoologische Beiträge* **42**, 241–51.

Janis CM (1990). Correlation of cranial and dental variables with body size in ungulates and macropodoids. In: Damuth J, MacFadden BJ, eds *Body Size in Mammalian Paleobiology: Estimations and Biological Implication.* Cambridge University Press, Cambridge, pp. 255–300.

Jessop TS, Madsen T, Sumner J, Rudiharto H, Phillips, JA, Ciofi C (2006). Maximum body size among insular Komodo dragon populations covaries with large prey density. *Oikos* **112**, 422–9.

Köhler M, Moyà-Solà S (2004). Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. *Brain Behaviour* **63**, 125–40.

Kostopoulos D, Palombo MR, Alberdi MT, Valli AM (2007). Pliocene to Pleistocene large mammal diversity and turnover in North Mediterranean region: Greek, Italian and Iberian Peninsula. *Geodiversitas* **29**, 401–19.

Kuss SE (1970). Abfolge und Alter der pleistozänen Säugetierfaunen der Insel Kreta. *Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau* **60**, 35–83.

Lax EM (1996). A Gazetteer of Cretan paleontological localities. In: Reese DS, ed. *Pleistocene and Holocene Fauna of Crete and its First Settlers*. *Monography in World Archaeology* **28**, 1–132.

Legendre S (1986). Analysis of mammalian communities from the late Eocene and Oligocene of Southern France. *Palaeovertebrata* **16**, 191–212.

Legendre S (1989). Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocéne) d'Europe occidentale: structures, milieux et ´évolution. *Münchner Geowissenchaftliche Abhandlungen* **16**, 1–110.

Lomolino MV (2005). Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* **32**, 1683–99.

Lomolino MV, Sax DF, Riddle BR, Brown JH (2006). The island rule and a research agenda for studying ecogeographical patterns. *Journal of Biogeography* **33**, 1503–10.

Lomolino M V, Weiser R (2001). Towards a more general species–area relationship, diversity on all islands, great and small. *Journal of Biogeography* **28**, 431–45.

Maiorana VC (1990). Evolutionary strategies and body size. In: Damuth J, MacFadden BJ, eds. *Body Size in Mammalian Paleobiology Estimation and Biological Principles*, Cambridge University Press, Cambridge, pp. 69–102.

Mangano G (2007). I depositi a vertebrate continentali del Pleistocene della calabria. *Atti dell'Accademia Peloritana dei Pericolanti. Classe di Scienze Fisiche, Matematiche e Naturali* **85**, 1–11.

Mappes T, Grapputo A, Hakkarainen H *et al.* (2008). Island

selection on mammalian life-histories: genetic differentiation in offspring size. *BMC Evolutionary Biology* **8**, 296.

Marquet PA, Taper ML (1998). On size and area, patterns of mammalian body size extremes across landmasses. *Evolutionary Ecology* **12**, 127–39.

Masini F, Petruso D, Bonfiglio L (2008). Origination and extinction patterns of mammals in three Central Western Mediterranean Islands in the Late Miocene to Quaternary. *Quaternary International* **182**, 63–79.

Mayhew DF (1977). The endemic Pleistocene Murids of Crete. I–II. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen* **80**, 182–214.

Mayhew D F (1996). The extinct murids of Crete. In: Reese DS, ed. *Pleistocene and Holocene Fauna of Crete and its first Settlers*. *Monography in World Archaeology* **28**, 167–71.

Meiri S, Cooper N, Purvis A (2008). The island rule: made to be broken? *Proceedings: Biological Sciences* **275**, 141–8.

Meiri S, Dayan T, Simberloff D (2004). Body size of insular carnivores, little support for the island rule. *American Naturalist* **163**, 469–79.

Meiri S, Dayan T, Simberloff D (2005a). Area, isolation, and body size evolution in insular carnivores. *Ecological Letters* **8**, 1211–7.

Meiri S, Simberloff D, Dayan T (2005b). Insular carnivore biogeography: island area and mammalian optimal body size. *American Naturalist* **165**, 505–14.

Meiri S, Dayan T, Simberloff D 2006. The generality of the island rule re-examined. *Journal of Biogeography* **33**, 1571–7.

Millien V (2006). Morphological evolution is accelerated among island mammals. *PLos Biology* **4**, 1863–8.

Mills MG, Moro D, Spencer PBS (2004). Conservation significance of island versus mainland populations: a case study of dibblers (*Parantechinus apicalis*) in Western Australia. *Animal Conservation* **7**, 387–95.

Mol D, de Vos J, van den Bergh G D, Sondaar PY (1996). The taxonomy and ancestry of the fossil elephants of Crete: Faunal turnover and a comparison with Proboscidean faunas of Indonesian Islands. In: Reese DS, ed. *Pleistocene and Holocene Fauna of Crete and its First Settlers*. *Monography in World Archaeology* **28**, 81–98.

Nor SM (1996). The mammalian fauna on the islands at the northern tip of Sabah, Borneo. *Fieldiana-Zoology* **83**, 1–51.

Palkovacs EP (2003). Explaining adaptive shifts in body size on islands: a life history approach. *Oikos* **103**, 37–44.

Palombo MR (1996). Large Pleistocene mammals of the Mediterranean islands. *Vie et Milieu* **46**, 365–74.

Palombo MR (2001). Paedomorphic features and allometric growth in Elephas falconeri skull from Spinagallo (Middle Pleistocene, Sicily). In: Cavaretta G, Gioia P, Mussi M, Palombo MR, eds *The World of Elephants*. Consiglio Nazionale delle Ricerche, Roma, pp. 492–6.

Palombo MR (2003). *Elephas, Mammuthus, Loxodonta*, who is the true ancestor of the dwarf elephant of Sicily? *Deinsea* **10**, 273–91.

Palombo MR (2005). Biochronology of the Plio-Pleistocene mammalian faunas of Italian peninsula: knowledge, problems and perspectives. *Il Quaternario* **17**, 565–82.

Palombo MR (2007a). How can endemic elephant help us in understanding "island rule"? *Quaternary International* **169–170**, 105–24.

Palombo MR (2007b). Large mammal guilds on the Italian Peninsula from the Pliocene to the Late Pleistocene: new methodological approaches. *Courier Forschungsinstitut Senckenberg* **259**, 13–46.

Palombo MR, Köhler M, Moya Sola S, Giovinazzo C (2008). Brain versus body mass in endemic ruminant artiodactyls; a case studied of *Myotragus balearicus* and smallest *Candiacervus* species from Mediterranean islands. *Quaternary International* **182**, 160–83.

Poulakakis N, Mylonas M, Lymberakis P, Fassoulas C (2002). Origin and taxonomy of the fossil elephants of the island of Crete (Greece): problems and perspectives. *Palaeogeography, Palaeontology, Palaeoecology* **186**, 163–83.

Poulakakis N, Parmakelis A, Lymberakis P *et al.* (2006). Ancient DNA forces reconsideration of evolutionary history of Mediterranean pygmy elephantids. *Biology Letters* **2**, 451–4.

Prothero DR, Sereno PC (1982). Allometry and palaeoecology of medial Miocene dwarf rhinoceroses from the Texas Gulf coastal plain. *Paleobiology* **8**, 16–30.

Raia P, Meiri S (2006). The island rule in large mammals: Paleontology meets Ecology. *Evolution* **60**, 1731–42.

Raia P, Barbera C, Conte M (2003). The fast life of a dwarfed giant. *Evolutionary morphology* **17**, 293–312.

Reese D S, Belluomini G, Ikeya M (1996). Absolute dates for the Pleistocene fauna of Crete. In: Reese D S, ed. *Pleistocene and Holocene fauna of Crete and its first settlers*. *Monographs in world archaeology* **28**, 47–51.

Reumer JWF (1980). On the Pleistocene shrew *Nesiotites hidalgo* Bate, 1944 from Majorca (Soricidae, Insectivora). *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen* B **83**, 39–68.

Reumer JWF, Oberli F (1988). Shrews (Mammalia, Soricidae) from a Bronze Age deposit in Cyprus, with the description of a new subspecies. *Bonner zoologische Beiträge* **39**, 305–14.

Rhodes EJ (1996). ESR dating of tooth enamel. In: Basile B, Chilardi S, eds *Le ossa dei Giganti. Lo scavo paleontologico di Contrada Fusco*, Arnaldo Lombardi, Siracusa, pp. 39–44

Roth VL (1981). Constancy of size ratios of sympatric species. *American Naturalist* **118**, 394–404.

Roth VL (1990). Insular dwarf elephants, a case study in body mass estimation and ecological inference. In: Damuth J, MacFadden BJ, eds. *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*. Cambridge University Press, Cambridge, pp. 151–79.

Schoener TW (1989). Food webs from the small to the large. *Ecology* **70**, 1559–89.

Scott KM (1990). Postcranial dimension of ungulates as predictors of body mass. In: Damuth J, MacFadden BJ, eds. *Body Size in Mammalian Paleobiology: Estimations and Biological Implication*. Cambridge University Press, Cambridge, pp. 301–36.

Sondaar PY, Van der Geer AAE (2005). Evolution and extinction of Plio-Pleistocene island ungulates. In: Crégut-Bonnoure E, ed. *Les ongulés holarctiques du Pliocène et du Pléistocene. Quaternaire, International Journal of the French Quaternary Association*, hors-série 2005, **2**, 241–56.

Spaan A (1996). *Hippopotamus creutzburgi*: The case of the Cretan *Hippopotamus*. In: Reese DS, ed. *Pleistocene and Holocene Fauna of Crete and its First Settlers*. *Monography in World Archaeology* **28**, 99–110.

Symeonidis N, Theodorou G, Gianopoulos B (2000). The new species *Elephas chaniensis* from the submerged Pleistocene deposits of Vamos Cave at Chania, Crete. *Bulletin de la Societe Speleologique de Grece* **22**, 95–108. (in Greek.)

Theodorou G (1983). The dwarf elephants of the Charkadio Cave on the island of Tilos (Dodekanese, Greece) (PhD dissertation). University of Athens, Athens.

Theodorou G, Symeonidis N, Stathopoulou E (2007). *Elephas tiliensis* n. sp. from Tilos island (Dodecanese, Greece). *Hellenic Journal of Geosciences* **42**, 19–32.

Tsoukala E, Lister A (1998). Remains of straight-tusked elephant, *Elephas (Paleoloxodon) antiquus* Falc. & Caut. (1847) ESR-dated to oxygen isotope Stade 6 from Grevena (W. Macedonia, Greece). *Bollettino della Società Paleontologica Italiana* **37**, 117–39.

Valverde JA (1964). Remarques sur la structure et l'évolution des communautés de vertébrés terrestres. I. Structure d'une communauté. II. Rapport entre prédateurs et proies. *Terre et Vie* **111**, 121–54.

Van Valen LM (1973). Pattern and the balance of nature. *Evolutionary Theory* **1**, 31–49.

Van Valkenburgh B (1990). Skeletal and dental predictors of body mass in carnivores. In: Damuth J, MacFadden BJ, eds, *Body Size in Mammalian Paleobiology, Estimation and Biology Implications*. Cambridge University Press, Cambridge, pp. 181–205.

Vrba ES (1995). On the connections between Paleoclimate and evolution. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, eds, *Paleoclimate and Evolution with Emphasis on Human Origins*. Yale University Press, New Haven and London, pp. 24–45.